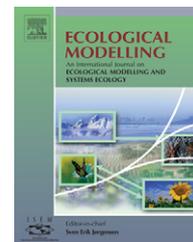


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Letter to the editor

Comments on “Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock”

Chaloupka and Balazs (2007) present a surplus production model ensemble consisting of a Bayesian state-space model and a stochastic simulation model, both based on a Pella–Tomlinson type surplus production model. The state-space model uses Markov chain Monte Carlo (MCMC) simulation to fit time series data for green turtle harvest and nesting abundance trends, resulting in posterior median and 95% credible intervals for the parameters of the Pella–Tomlinson model and harvest management measures. They then use *only* the median values of those posterior distributions in a stochastic Pella–Tomlinson type surplus production simulation model to assess the population response, in terms of nester abundance, to different harvest levels. The stochasticity incorporated in the surplus production model and suggested in the plots presented in their Fig. 8 results from lognormal process and stochastic observation error incorporated into the surplus production model rather than any incorporation of uncertainty surrounding the parameter values estimated by the Bayesian state-space model.

The approach taken by Chaloupka and Balazs (2007) is inventive in that it applies fisheries stock assessment methods to the assessment of sea turtle stocks, integrating two datasets, pre-Endangered Species Act listing annual harvest rates and annual nesting beach counts. This is a novel approach in the analysis of sea turtle population dynamics and will hopefully lead to similar and more refined efforts. I believe, though, that the authors go too far in suggesting that this modelling approach is robust enough to be a management tool and a basis for recommending harvest levels.

The results of their modelling efforts suggest strong evidence that the Hawaiian green turtle population is close to full recovery, with median posterior values for the 2004 biomass fraction of carrying capacity (ratio of biomass to carrying capacity) ranging from 73 to 90%. Projections of their stochastic simulation model suggest that the population, as indexed by annual nesting female abundances (nesters), will abruptly level off in 2005 (see their Fig. 8). The models suggest median

maximum annual surplus production of 18–30 tonnes and that the current standing biomass (as of 2004) is sufficient to initiate a harvest. Chaloupka and Balazs (2007) suggest that a limited harvest of up to 10 tonnes/year could now be initiated without negative impact on the population.

For the Bayesian state-space model of Chaloupka and Balazs (2007), the posterior distributions of carrying capacity (K) are essentially the same as the prior distributions, which indicates that the data are not informative for this parameter, a point which the authors readily admit. As the key management parameters resulting from their model depend on K , an understanding of K in relation to the current population biomass is critical to the application of, and management inferences from, the surplus production model used. However, their model does not provide convincing evidence that the population is near K . Indeed, if one looks at the plot of nester abundance in their Fig. 1b and c (and here in Fig. 1), the population appears to still be growing exponentially. The spline curve in their Fig. 1c gives no suggestion of a population approaching carrying capacity.

A standard method in Bayesian modelling is posterior predictive checking where observed data are compared to those generated by the model fit, and systematic discrepancies between simulated and observed data suggest potential failings of the model (Gelman et al., 2004). While the exact application of this method can take different forms (Gelman et al., 2004), one approach is to omit some of the observed data, fit the model to the remaining data, and forecast the omitted data to determine how well the model approximates the omitted data (Gelman et al., 2004; Rivot et al., 2004; Larssen et al., 2007). The predictive ability of the Bayesian state-space model of Chaloupka and Balazs (2007) is easily evaluated with this approach and I apply it by using subsets of the nester abundance data, fitting the Bayesian state-space model of Chaloupka and Balazs (2007) to different time series of the nester data, 1973–1999 and 1973–1994 to test how well the model predicts trends

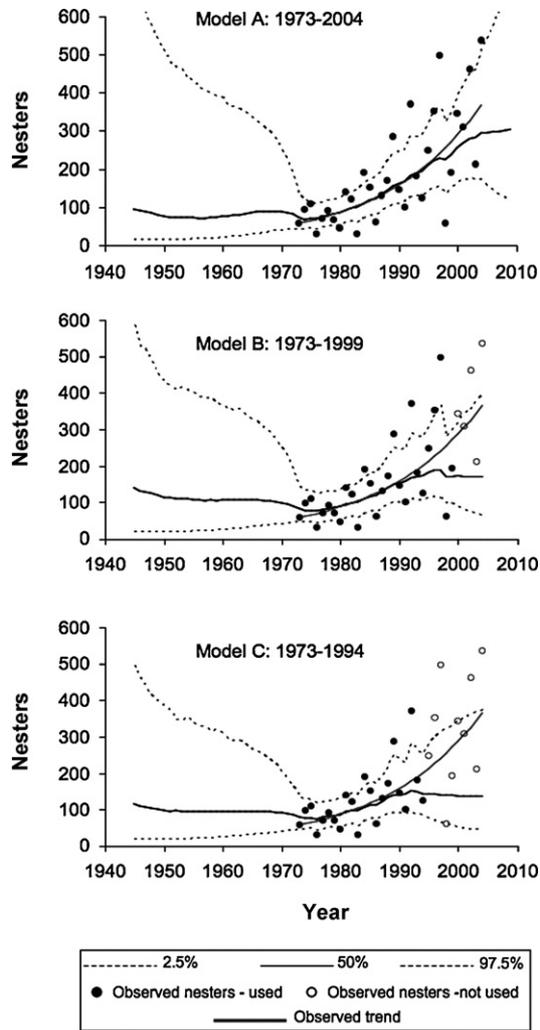


Fig. 1 – Summary of the Bayesian state-space model fits for nester data for Models A–C. Dashed lines show the 95% credible intervals and the solid black line shows the median values, or the median predicted trend. Circles represent the observed nester data from 1973 to 2004, filled circles highlight which data were used in the model fitting, 1973–2004 for Model A, 1973–1999 for Model B and 1973–1994 for Model C. The gray solid line is an exponential curve fit to the 1973–2004 nester data and represents the observed trend. This curve gives a fit similar to the spline curve used in Chaloupka and Balazs (2007, see their Fig. 2e).

in nester abundance for the time periods 2000–2004 and 1995–2004.

I repeated the Bayesian state-space model presented by Chaloupka and Balazs (2007), using the WinBUGS code provided in their appendix. I estimated the harvest and nester abundance data from their Fig. 1a and b using digiMatic® software. Following Chaloupka and Balazs (2007), for the MCMC simulations in WinBUGS, I used a 50,000 burn-in sample and 250,000 additional iterations, sampling every 25th sample for a total of 10,000 samples. For the models presented here, convergence diagnostics were performed on two separately initialized chains using the Bayesian output analysis (BOA) package

for S-Plus (Smith, 2004), and the models passed convergence and stationarity diagnostics. To demonstrate that the data and modelling procedures are comparable to those used by Chaloupka and Balazs (2007), I replicated their Model 1 and achieved similar results (Table 1; compare Model 1 to Model A). Again using the prior distributions as defined for Model 1; I fit the Bayesian state-space model to nester abundance data from 1973 to 1999 (deleting the last 5 years of data; Model B) and from 1973 to 1994 (deleting the last 10 years of data; Model C), then forecasted the nester abundance through 2004. For Model A, I forecasted nester abundance data through 2009.

The predictive abilities of Models B and C were poor, both suggested that the population was near K at the end of the time series (Tables 1 and 2) and that the nester abundance trends should rapidly stabilize, however the additional years of nester abundance data do not support this leveling trend (Fig. 1). Similarly, Model A, with nester abundance forecasted through 2009, predicts rapid stabilization at the end of the time series (as does Model 1 of Chaloupka and Balazs, 2007, see their Fig. 8), however given the poor predictive abilities of Models B and C, and the fact that the observed data do not suggest a leveling trend, this is likely not a valid result (Fig. 1). For Model B, all five of the observed data points beyond the end of the fitted time series were above the median predicted values and three of the five were above the 95% credible interval (Fig. 1). For Model C, 9 of the 10 observed values beyond the end of the time series were above the median predicted values and 5 of the 10 were above the 95% credible interval (Fig. 1).

These results are disturbing considering that Model A (or Model 1 of Chaloupka and Balazs, 2007) is being used to recommend a harvest level. For Model A, using the full time series of nester data from 1973 to 2004, the median value of the biomass fraction of carrying capacity in 1994 and 1999 was estimated at 52 and 64%, respectively. However, Model B, using nester data from 1973 to 1999, estimated the median value of the biomass fraction of carrying capacity in 1999 at 93% and Model C estimated this value in 1994 at 97% (Table 1). Both of the truncated time series suggest that the population was at carrying capacity at the end of the time series but additional years of data demonstrated that the population was in fact still well below carrying capacity. Furthermore, while Models B and C both suggested that the biomass at the end of their respective time series was sufficient to initiate a harvest, with maximum surplus production values similar to those reported for Model 1 in Chaloupka and Balazs (2007), 26 and 28 tonnes, as compared to 30 tonnes (Table 1), the additional years of data used in Model A showed that the biomass at those times, 1994 and 1999 would not have been sufficient for harvest (Table 1). Rather, 10 years of additional data demonstrated that the population continued to grow exponentially through 2004 (Fig. 1). If we rerun this model in another 5–10 years, will we find the same result, that in 2004 the population was in fact not close to its carrying capacity and the biomass was not sufficient to initiate a harvest? Although Larssen et al. (2007) found increasing accuracy with increasing length of the time series used, from Fig. 1, the answer seems likely to be yes. Based on the apparent exponential trend in the nester data (Fig. 1), this population appears to still be recovering and may be well below its carrying capacity.

Table 1 – Median values of the posterior distributions achieved from the Bayesian state-space model presented by Chaloupka and Balazs (2007)

	Model 1	Model A	Model B	Model C
Carrying capacity (K, tonnes)	1431.0	1430.0	1317.0	1398.0
Intrinsic population growth (r)	0.054	0.055	0.054	0.055
Abundance index scaling factor (q)	0.287	0.306	0.147	0.110
Production function shape parameter (z)	2.94	2.91	2.62	2.59
Biomass in 1944 (tonnes)	329.0	446.5	1251.0	1273.0
Biomass in 1973 (tonnes)	278.8	231.5	529.5	699.7
Biomass in 1994 (tonnes)	NR	637.8	1152.0	1284.0
Biomass in 1999 (tonnes)	NR	774.9	1133.0	1241.0
Biomass in 2004 (tonnes)	1073.0	963.6	1096.0	1213.0
Biomass fraction of K in 1944 (productivity)	0.269	0.391	1.216	1.120
Biomass fraction of K in 1973	0.212	0.183	0.426	0.540
Biomass fraction of K in 1994	NR	0.515	0.949	0.967
Biomass fraction of K in 1999	NR	0.638	0.932	0.943
Biomass fraction of K in 2004	0.834	0.810	0.916	0.936
MSP (maximum surplus production, tonnes)	30.4	29.8	26.1	28.4
Bmsp (biomass at MSP, tonnes)	897.6	887.0	800.2	845.3
Fmsp (harvestable fraction at MSP)	0.034	0.034	0.032	0.034
Fraction of harvest reported ($\gamma = \text{beta}(\alpha, \beta)$)	0.506	0.524	0.488	0.501
α hyperparameter for harvest report rate, beta pdf	51.85	53.64	48.72	51.00
β hyperparameter for harvest report rate, beta pdf	50.34	47.89	51.65	50.55
Process error variance (σ^2)	0.008	0.008	0.019	0.018
Observation error variance (τ^2)	0.293	0.326	0.360	0.309

Model 1 shows the results presented by Chaloupka and Balazs (2007), their Table 2. Model A shows the results achieved using the WinBUGS code in Chaloupka and Balazs (2007) Appendix A, the same priors as for their Model 1, and the data for harvest and nester abundance estimated from their Fig. 1a and b for 1973–2004. Model B is the same as Model A, but using only the 1973–1999 nester abundance data, similarly Model C uses the 1973–1994 nester abundance data. NR indicates ‘not reported’. Bold numbers are outside the range of data used to fit the model and are predictions.

Table 2 – Posterior means and percentiles for the model and management parameters resulting from the three models discussed in the text

Parameter	Mean	S.D.	Percentiles		
			2.5%	Median	97.5%
Model A					
Carrying capacity (K, tonnes)	1910.0	1633.0	346.1	1430.0	6393.0
Intrinsic population growth (r)	0.057	0.015	0.032	0.055	0.089
Abundance index scaling factor (q)	0.529	0.700	0.048	0.306	2.354
Production function shape parameter (z)	2.96	1.13	1.09	2.91	4.85
Biomass in 1944 (tonnes)	1603.0	2636.0	87.3	446.5	8801.0
Biomass in 1973 (tonnes)	379.1	458.9	37.4	231.5	1602.0
Biomass in 1994 (tonnes)	1001.0	1163.0	81.3	637.8	4177.0
Biomass in 1999 (tonnes)	1178.0	1311.0	102.9	774.9	4678.0
Biomass in 2004 (tonnes)	1479.0	1654.0	138.5	963.6	6038.0
Biomass fraction of K in 1944 (productivity)	0.932	0.975	0.037	0.392	2.914
Biomass fraction of K in 1973	0.218	0.165	0.023	0.183	0.644
Biomass fraction of K in 1994	0.559	0.369	0.052	0.515	1.396
Biomass fraction of K in 1999	0.657	0.400	0.066	0.638	1.555
Biomass fraction of K in 2004	0.817	0.508	0.090	0.810	1.991
MSP (maximum surplus production, tonnes)	41.5	39.0	6.5	29.8	151.2
Bmsp (biomass at MSP, tonnes)	1184.0	1024.0	209.9	887.0	4051.0
Fmsp (harvestable fraction at MSP)	0.035	0.009	0.019	0.034	0.055
Fraction of harvest reported ($\gamma = \text{beta}(\alpha, \beta)$)	0.529	0.225	0.106	0.524	0.951
α hyperparameter for harvest report rate, beta pdf	53.03	27.51	6.30	53.64	97.82
β hyperparameter for harvest report rate, beta pdf	48.74	28.65	3.19	47.89	97.07
Process error variance (σ^2)	0.021	0.036	0.001	0.008	0.114
Observation error variance (τ^2)	0.342	0.101	0.195	0.326	0.584
Model B					
Carrying capacity (K, tonnes)	1741.0	1466.0	306.0	1317.0	5621.0
Intrinsic population growth (r)	0.056	0.017	0.030	0.054	0.098

Table 2 (Continued)

Parameter	Mean	S.D.	Percentiles		
			2.5%	Median	97.5%
Abundance index scaling factor (q)	0.258	0.427	0.028	0.147	1.053
Production function shape parameter (z)	2.74	1.11	1.07	2.62	4.82
Biomass in 1944 (tonnes)	2100.0	2831.0	126.8	1251.0	9335.0
Biomass in 1973 (tonnes)	803.7	897.9	75.4	529.5	3247.0
Biomass in 1994 (tonnes)	1642.0	1683.0	161.6	1152.0	6177.0
Biomass in 1999 (tonnes)	1598.0	1635.0	177.5	1133.0	5848.0
Biomass fraction of K in 1944 (productivity)	1.276	0.895	0.086	1.216	3.047
Biomass fraction of K in 1973	0.466	0.253	0.069	0.426	1.023
Biomass fraction of K in 1994	0.945	0.428	0.168	0.949	1.903
Biomass fraction of K in 1999	0.922	0.390	0.191	0.932	1.751
MSP (maximum surplus production, tonnes)	36.2	34.3	5.5	26.1	125.9
Bmsp (biomass at MSP, tonnes)	1061.0	904.0	183.1	800.2	3423.0
Fmsp (harvestable fraction at MSP)	0.034	0.011	0.018	0.032	0.059
Fraction of harvest reported ($\gamma = \text{beta}(\alpha, \beta)$)	0.489	0.235	0.071	0.488	0.939
α hyperparameter for harvest report rate, beta pdf	49.53	28.55	4.36	48.72	97.35
β hyperparameter for harvest report rate, beta pdf	51.26	28.41	3.69	51.65	97.87
Process error variance (σ^2)	0.033	0.046	0.001	0.019	0.148
Observation error variance (τ^2)	0.385	0.137	0.193	0.360	0.724
Model C					
Carrying capacity (K , tonnes)	1832.0	1557.0	331.1	1398.0	5989.0
Intrinsic population growth (r)	0.058	0.018	0.030	0.055	0.100
Abundance index scaling factor (q)	0.174	0.214	0.021	0.110	0.715
Production function shape parameter (z)	2.73	1.11	1.08	2.59	4.82
Biomass in 1944 (tonnes)	2119.0	2624.0	138.3	1273.0	9275.0
Biomass in 1973 (tonnes)	1039.0	1083.0	104.1	699.7	3963.0
Biomass in 1994 (tonnes)	1790.0	1758.0	219.9	1284.0	6521.0
Biomass fraction of K in 1944 (productivity)	1.215	0.858	0.096	1.120	2.974
Biomass fraction of K in 1973	0.566	0.278	0.121	0.540	1.132
Biomass fraction of K in 1994	0.976	0.385	0.273	0.967	1.814
MSP (maximum surplus production, tonnes)	38.8	36.5	5.6	28.4	136.4
Bmsp (biomass at MSP, tonnes)	1113.0	955.9	197.0	845.3	3637.0
Fmsp (harvestable fraction at MSP)	0.035	0.011	0.018	0.034	0.060
Fraction of harvest reported ($\gamma = \text{beta}(\alpha, \beta)$)	0.504	0.228	0.085	0.501	0.947
α hyperparameter for harvest report rate, beta pdf	51.03	27.89	4.97	51.00	97.73
β hyperparameter for harvest report rate, beta pdf	50.63	28.58	3.34	50.55	97.68
Process error variance (σ^2)	0.036	0.063	0.001	0.018	0.170
Observation error variance (τ^2)	0.332	0.129	0.153	0.309	0.650

Model A: Priors as reported for Model 1 of Chaloupka and Balazs (2007). Nester abundance data from 1973–2004. Model B: Priors as reported for Model 1 of Chaloupka and Balazs (2007). Nester abundance data from 1973–1999. Model C: Priors as reported for Model 1 of Chaloupka and Balazs (2007). Nester abundance data from 1973–1994.

One of the benefits of using a Bayesian approach in a stock assessment is that it demonstrates the uncertainty associated with estimations of management parameters (Booth and Quinn, 2006). However, Chaloupka and Balazs (2007) used only the median values of the posterior distributions from the Bayesian state-space model for the parameters in the stochastic simulation model, even though the 95% credible intervals for these parameters are quite large (Table 2). The 2.5 percentile of the 95% credible interval for maximum surplus production for their Model 1 is 2.6 tonnes. How then, based on these results, can one conclude that a harvest of 10 tonnes will have a minimal impact on the population? For the same model, the 2.5 and 97.5 percentiles for the posterior distribution of biomass fraction of K were 13 and 185% of K , respectively. That the 95% credible interval shows results that range from critically depleted to nearly double carrying capacity should raise a red flag that this modelling exercise does not provide enough information about the population to under-

stand its dynamics and certainly not enough information to suggest the population can go from full protection under the U.S. Endangered Species Act to being a harvestable resource.

I applaud the authors for taking a unique and potentially useful approach to a stock assessment for a protected species. However, I believe that they have drawn management conclusions that are incautious and go beyond what the model and available data reliably support.

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